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ON A RESTORATION OF THE BASE OF THE CRANIUM OF *HESPERORNIS REGALIS*

BY R. W. SHUFELDT

In so far as I am aware, there has not, up to the present time, been published a figure giving the probable appearance, and the various bony parts, of the cranium of that great, extinct, loon-like diver of Cretaceous times — Marsh's *Hesperornis regalis*. Disregarding a text-cut on page 9 of the "Odontornithes," Marsh gives us, on Plate I of that work, but two natural-size views of the cranium of *H. regalis* which show the lost parts restored in outline. These figures I have carefully studied and compared with several skulls of the Loon (*Gavia immer*), belonging to the collection of the United States National Museum; further, I have compared the former as well as the latter with a series of photographs, sent me by Mr. Gerhard Heilmann, of Copenhagen, which photographs were made of the cranium of the type specimen of *H. regalis* in the Peabody Museum of Yale University, under the direction of Professor Richard S. Lull. These are helpful, in the absence of the actual specimen; though not as much as they might be had they been obtained by a photographer of experience. Unfortunately, no attention was paid to lighting, to point of view, or to the matter of reproduction of detail, while they show fairly well several other points. Lastly, to aid one in restoring the base of the cranium of *Hesperornis regalis*, there are to be found still other illustrations in the "Odontornithes." We have, on Plate II of the work, no fewer than twelve figures devoted to the teeth and osseous structures at the *basis cranii*; these will be duly commented upon as they are taken up in detail and associated in the restoration here to be made.

Evidently, the first step to be undertaken is to obtain a correct *outline* of the base of the cranium, as the details *within* such an outline may be filled subsequently. To obtain this, I made a careful tracing on transfer paper of Marsh's Fig. 5 of Plate I of the "Odontornithes," which represents, natural size, the "skull" of *Hesperornis regalis*, seen directly from above. With the mid-longitudinal axis of the cranium parallel to the plane upon which the latter rests; the point of view from above being at the proper distance to avoid the distortion caused by being too near, and in a line perpendicular to the aforesaid plane, crossing at its middle point the transverse diameter of the cranium situated at an equal distance between its two extremities—is presumably the view given in Fig. 5 of Plate I ; so that, if the cranium were turned completely over and placed in the same position just described, the *outlines* seen would be identical, provided we regarded the cranium when thus placed from the *same* viewpoint. Therefore, the tracing I made of the outline of the superior view shown in Fig. 5, would be equally accurate for the corresponding inferior or ventral view of this cranium, and likewise be of natural size.

Fig. 1 of Plate II of the "Odontornithes" presents the inferior surface of the premaxillary and maxillary bones, with a tooth (*t*) in the groove of the latter on the left side. This drawing I take to be an accurate one, for the reason that all of its outlines agree with those of the same parts shown in Fig. 5, Plate I for the superior view; consequently, as far as it would carry, I used it in my restoration, which latter illustrates the present article.

The cultrate margins of the superior osseous mandible (*pmx*) were formed by the premaxillary bone, and, upon either side, they extended backwards for a distance of 8.9 cms., terminating at the maxillo-premaxillary suture, which is distinctly shown in the accompanying Plate. At this point the superior osseous mandible has a transverse diameter of 1.75 cms.; and at a distance of one centimeter upon either side, posterior to it, the grooves for the teeth commenced. Each of these grooves measured antero-posteriorly, 5.2 cms., and had implanted in them, in the manner described by Marsh; fourteen teeth. Either groove is nearly straight, and lies entirely in the outer inferior part of the maxillary bone on either side. The free apices of these teeth are directed downwards and backwards, and their description has been given in great detail in the "Odontornithes."

Between the first and the ninth tooth on either side – the most anterior tooth being considered the first – the median portion of the premaxillary has an average width or transverse diameter of one centimeter; and, as the mesial margins of the prepalatines (*pp*) are somewhat further apart than this – though they approach each other anteriorly and posteriorly – a long spindle-shaped hiatus results upon either side of the premaxillary.

These hiatuses are also to be observed in Marsh's Fig. 5 of Plate I of the "Odontornithes," where they have precisely the same positions and apertural extent. In this figure, too, we have the point indicated, upon either side, where the *maxillary* (*mx*) gradually commences to broaden. This is as it is in most *Colymbidæ* and *Gaviidæ*, and in all probability is quite correct.

Posterior to these maxillary expansions we have the remainder of the *quadrato-jugal* bar upon either side (*j–qj*); and, as we have the posterior or *quadro-jugal* portions of these, there can be no doubt but that the *jugal* extension forward, to join the maxillary in the case of either bar, was as we find it in *Gavia immer* or the Loon of the existing avifauna, the restoration of the infraorbital bar, as shown in my figure, from the maxillary(*mx*) to the quadrate(*qu*) must then be entirely correct. Marsh figures the quadrato-jugal portions in the "Odontornithes" (Pl. I, Fig. 1 and 5, *qj*). With respect to the *premaxillary* (*pmx*) he says that they "are elongate, and separate throughout their posterior two-thirds (Pl. I, Fig. 5). Their extremities touched the frontals. Their sides are deeply excavated for the anterior nares, and in front they are ankylosed, and form a long pointed beak, the end of which is somewhat decurved. This extremity, back to the nasal openings, has its surface fitted with irregular vascular foramina, indicating, apparently, that it was once covered with a horny bill, as in modern birds." (P. 8.)

This part of his description is probably quite accurate; and as far as it applies to a ventral view of the superior mandible, I have adhered to it in my restoration, as shown on the accompanying Plate. It is all the more acceptable and likely to be correct, in as much as he, Marsh, seems for the moment to have lost sight of the ostrich or ratite skull he forever had in mind, while describing the skeleton of this great, extinct, Cretaceous diver or loon. As he makes no mention whatever of the *maxillo-palatines* (*mxp*), it is fair to presume that those delicate structures were not found to be present in the fossil remains of *Hesperornis;* but, as there is every reason to believe that the bird possessed them in its skull, I have restored them according to what we find, with respect to their morphological character, in the skulls of the *Pygopodes* found in the existing avifauna of this and other countries. They were most likely elongate, scroll-like bones that were well separated in the median line of the cranium.

Turning to the vomerine ossification, Marsh tells us, on page 7 of the "Odontornithes," that "The vomers in *Hesperornis* are separate, as in lizards and a few existing birds. They are smaller than the palatines, and resemble the vomers of *Rhea*, more than those of the other *Ratitæ*. They are broadest at the base, which is obliquely truncated, and they taper gradually to the pointed extremity in front (Plate II, figure 8). The thick, posterior end may possibly have united with the pterygoid, as well as with the palatine. Both vomers are preserved in the skull figured on Plate I, but are displaced." It is true, to be sure. that we find double and independant vomers commonly among lizards ; but there are no existing birds with separate, twin vomers. The late Prof. William Kitchen Parker believed that they so existed in the skulls of the woodpeckers (*Picidæ*) ; but he was mistaken in regard to it, as both Garrod and I subsequently demonstrated. Professor Huxley entertained the same opinion that Professor Parker did ; but, as the latter states, he had very indifferent material to study for the determination of such a point.*

Personally I do not believe the vomers were separate in *Hesperornis*, but that they were simply broken apart in the specimens Marsh examined. As to their resembling the "vomers of *Rhea*," I may say that this is by no means the case, and much less do they in any way whatever resemble the vom-

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*Huxley, Thomas H. : "On the Classification of Birds ; and on the Taxonomic Value of the Modifications of Certain of the Cranial Bones Observable in that Class." *P. Z. S., 1867, pp. 448-449, fig. 30.*

Parker, W. K., ; "On the Picidæ." *Trans. Linn. Soc., 1875, Ser. 2, vol. 1, pls. 1-5 ;* also article, "Birds", *Encycl. Brit., 9th ed., vol. iii, p. 716.*

er of an Ostrich.* (See Plate 2.)

In *Gavia immer* the two halves of the single, median vomer are easily broken apart, and each part might easily be mistaken for a *single* vomer. Marsh's figures of "vomers" of *Hesperornis* are evidently the *halves* of a single, median, vomerine ossification. ("Odontornithes," Pl. II, fig's 8, 8a)

In restoring the *lacrymals*, I have followed Marsh's figures and description ; he says : "The lachrymal bone is distinct, and articulates with the frontal, nasal, and maxillary."(*Loc. cit.*, p. 7.) (See fig. 1, *l*.)

Passing to the *palatines*(fig's 1 and 2, Pl. II), Marsh says of them that they "resemble those of the Ostrich. They are long, slender bones, extending from their union with the pterygoids, parallel with the axis of the skull, and joining the premaxillaries. In one specimen they nearly lie in position, the left palatine being immediately beneath the left maxillary. In front of their junction with the pterygoid, and just anterior to their widest expansion, there is a deep pocket, very similar to that in the palatine of the Ostrich. The anterior half of the bone is slender and tapers gradually to the extremity." (*Loc. cit.*, p. 7.)

The "pocket" Marsh refers to would probably not be in view upon basal aspect of the cranium any more than it is in the Ostrich. Such a *fossa* in the *palatine* is found in a number of the *Pygopodes*, and even exists in the Grebes (*Podiceps cristatus*, No. 18,295, Coll. U. S. Nat. Mus.). The palatines of *Hesperornis* in no way whatever resembled those bones as we find them in the Ostriches, as any one will appreciate upon comparing them in Pls. 1 and 2 of the present article.

Indeed, no two birds' skulls, either of existing or extinct spe-

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Garrod, A. H. : "Notes on some of the Cranial Pecularities of the Woodpeckers." *Ibis, Oct., 1872, pp. 367-70.*

Shufeldt, R. W. : "On the Question of Saurognathism of the Pici, and and other Osteological Notes upon that Group." *P. Z. S., London, pt. 1, Feb. 3, 1891, pp. 122-129.*

*Huxley, T. H. : *loc. cit. ; figs. 1 and 2, pp. 420 - 421.* Excellent cuts of the basal views of the skulls of *Struthio camelus* and *Rhea americana* are given here. While the vomers in these Ratite birds are very different from each other, they do agree in some particulars.

cies could be more unlike each other than are the skulls of an *Hesperornis* and an Ostrich—the former being a toothed, Cretaceous loon, and the latter a recent, toothless, gigantic, struthian land-bird. Their skulls are about as unlike each other as are those of a hummingbird and a kiwi.

It will be observed that, in getting the outline and restoring the form of the frontal region of *Hesperornis* (Fig. 1 *pf*, *fr*,), I have followed Marsh, in as much as the outline was obtained by a tracing of Fig. 5, Plate I, as pointed out in a former paragraph of the present article.

Marsh states, on page 6 of the "Odontornithes," that "the posterior ends of palatines,and the anterior ends of the pterygoids are very imperfectly, or not at all, articulated with the basisphenoid rostrum;" and then, as I have already said, he again points out, on page 7, that the palatines "are long, slender bones, extending from their union with the pterygoids, parallel with the axis of the skull, and joining the premaxillaries." This does not militate against each pterygo-palatine articulation *resting* upon the base of the sphenoidal rostum, or just beyond its base, as I have shown it in Pl. 1 of this article. In fact, if the long axes of the palatines were *parallel* to the "axis of the skull," as Marsh states was the case, and, as he also states they had a "union with the pterygoids," they must have been placed as I have them in Plate 1, or quite like they are in the loons and other pygopodine birds. From Plate 1 it will be noted, too, that I have restored still another character given us by Marsh ; that is, there are present "strong 'basipterygoid' processes, arising from the body of the basisphenoid, and not from the rostrum, articulating with facets which are situated nearer the posterior than the anterior end of the inner edges of the pterygoid bones." (P. 6.)

As to the *pterygoids* and *quadrates* themselves, I have restored them as best I could from Marsh's figures and contour lines. He noted that the "upper, or proximal, articular head of the qudrate bone is not divided into two distinct heads," (P.6.) and this is an important point. There is no question as to his view with respect to the position of the *orbital processes* of the quadrates, for they are given in Fig. 5 of Plate I of the "Odontornithes,'' while the basal or ventral view of the left quadrate is shown on Plate II. (*6. c.*). His representation of the "right pterygoid bone'' is somewhat remarkable (Pl. II, figs. 7, 7a and 7b), and I have restored it as best I could. From Marsh's account, there is no question about its meeting the proximal end of the corresponding palatine, about its articulating with a stout facet found on the basisphenoid, and about its articulation with the pterygoidal process of the quadrate of the same side.

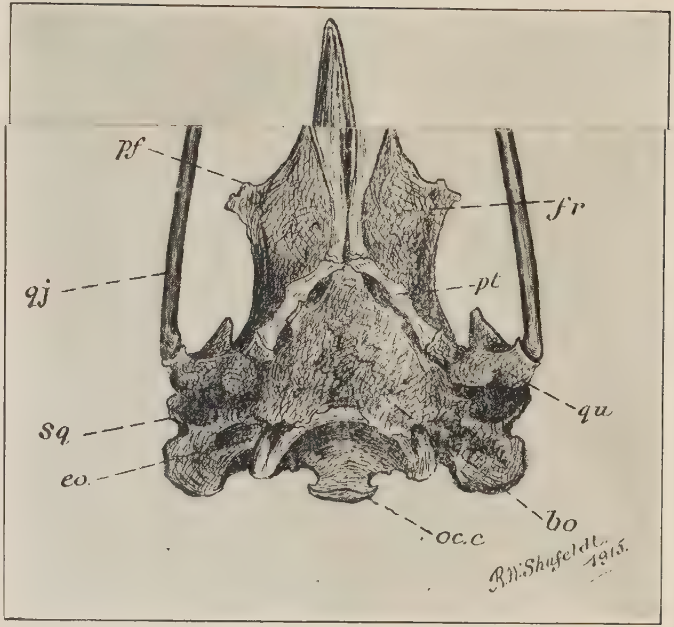
In restoring the hinder portion of the base of the cranium, I was entirely guided by Figure 5 of Plate II of the "Odontornithes,'' though I must add that I am by no means convinced as to its correctness. As Fig. 5 of Plate I in that work is given natural size as well as Fig. 5 of Plate II, both being viewed directly from above, it is clear that the *outline* of the posterior part of one should be precisely the same as the *outline* of the other. This, however, is not the case. I am therefore in doubt as to the details being correct, though at this writing it is the best I can offer in view of the fact that there are not at hand the actual specimens I should have. In any event, it will form a basis for improved restorations in the future, the importance of which will not be questioned by the vertebrate paleontologist. There is one thing, however, which the present article will accomplish : it will once and for all disabuse the mind of the paleornithologist with respect to there being any agreement of characters, when we come to compare the skull of an ostrich with that part of the skeleton of *Hesperornis*.

EXPLANATION OF PLATE I. (13)

Restoration of the *basis cranii* of *Hesperornis regalis*.

pmx, premaxillary ; *pp*, prepalatine ; *mxp*, maxillo-palatine ; *mx*, maxillary ; *f*, frontal ; *v*, vomer : *l*, lacrymal ; *j*, jugal ; *pl*, palatine ; *pf*, postfrontal process ; *fr*, frontal ; *qj*, quadrato-jugal ; *pt*, pterygoid; *qu*, quadrate ; *sq*, squamosal ; *eo*, exoccipital ; *bo*, basioccipital ; *oe. c*, occipital condyle.

(Reduced ; the amount of reduction being easily estimated from the measurements given in the text.)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R.W. Shufeldt. 1915.

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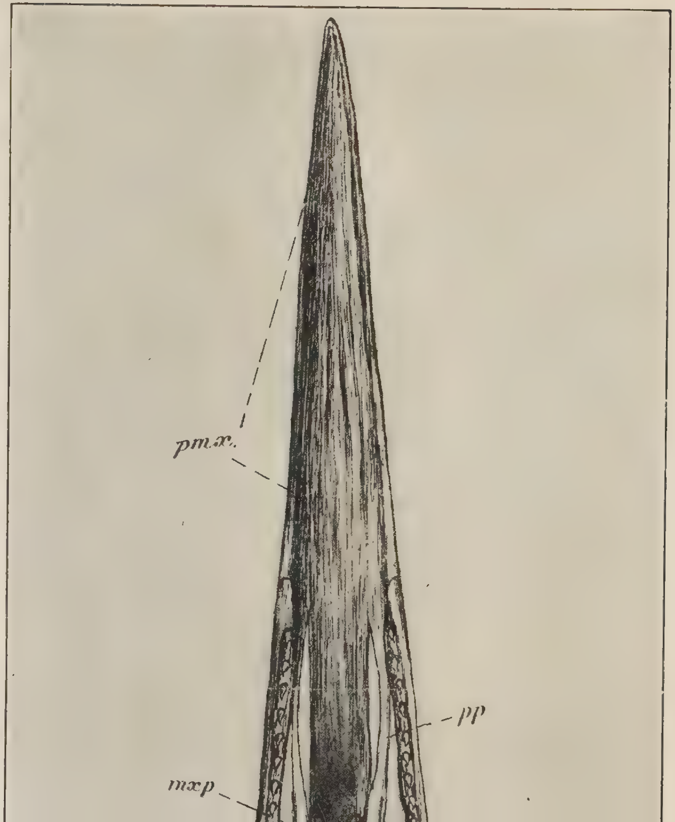
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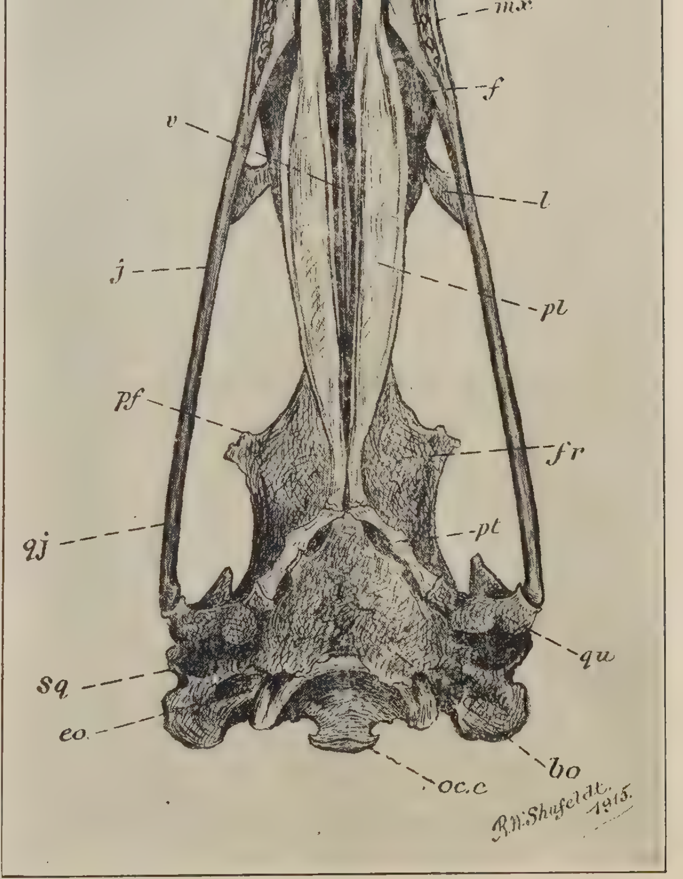
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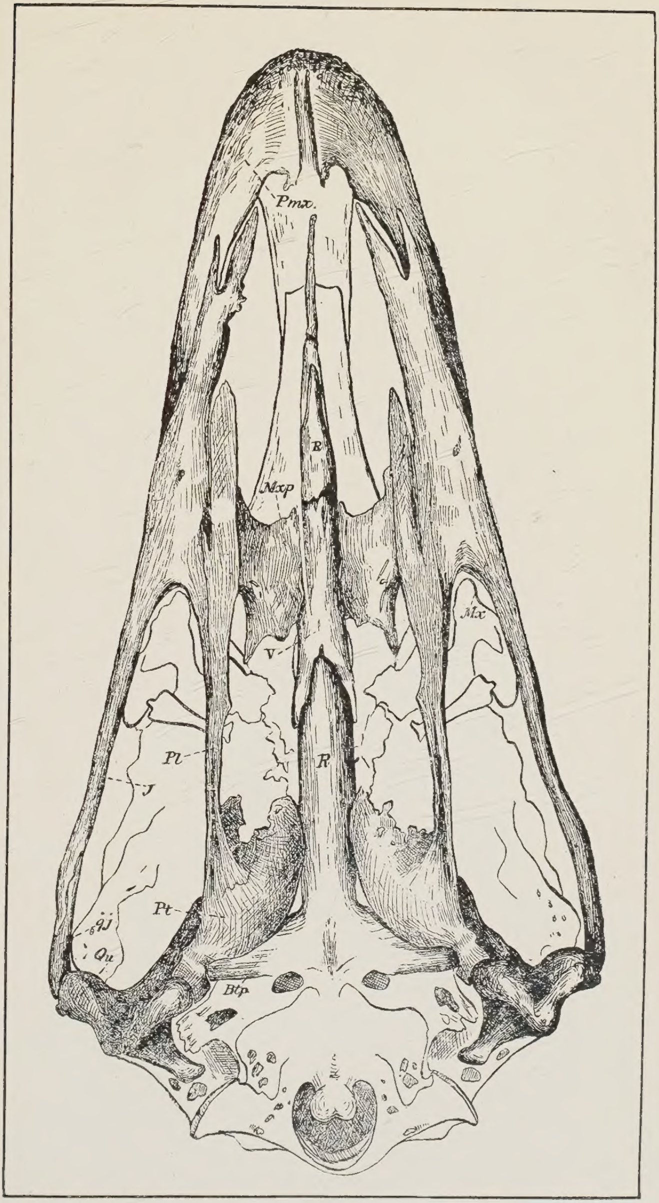
R.W. Shufeldt. 1915.

EXPLANATION OF PLATE 2 (14)

Basal view of the skull of the Ostrich (*Struthio camelus*) ; ¾ nat. size. By the author, from specimen No. 16,629, Coll. U. S. National Museum. *Btp*, basipterygoid ; *Qu*, quadrate ; *qj*, quadrato-jugal ; *Pt*, pterygoid : *j*, jugal ; *Pl*, palatine ; *R*, rostrum ; *v*, vomer ; *Mx*, maxillary; *Mxp*, maxillo-palatine ; *Pmx*, premaxillary.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